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NEONATE CODLING MOTH LARVAE (LEPIDOPTERA: TORTRICIDAE) ORIENT ANEMOTACTICALLY TO ODOR OF IMMATURE APPLE FRUIT

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Abstract.—Neonate codling moth larvae, *Cydia pomonella* (L.) responded positively to the odor of immature apples in an enclosed arena bioassay, in a Y-tube olfactometer, and in a straight tube olfactometer. In the arena bioassay, larvae contacted paper strips treated with apple odor. In the Y-tube olfactometer, larvae moved upwind and into the olfactometer arm carrying apple odor. In the straight tube olfactometer, larvae moved farther upwind per unit time in response to apple odor. Larval orientation to apple odor appeared to involve both an increase in forward speed (orthokinesis) and turning into airflow with increased odor concentrations (chemotaxis).

Key Words.—Insecta, Tortricidae, codling moth, attraction, host-finding

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The codling moth, *Cydia pomonella* L. is a key pest of apple (*Malus Xdomestica* Borkh) throughout much of the world. It is also a pest of pear (*Pyrus communis* L.) and walnut (*Juglans* sp.) and utilizes quince (*Cydonia oblonga*) and crab apple (*Malus* sp) among others (Metcalf et al. 1962).

Host finding and host selection by codling moths may be achieved in part by the female moth and in part by the larva. Adult female codling moth probably select host plants as oviposition sites, although little is known of how they locate or recognize hosts. Adult females oviposit primarily on foliage of host trees near fruit and infrequently on host fruit (Geier 1963, Putnam 1962, Wearing et al. 1973, Jackson 1978). Egg laying is stimulated by apple volatiles (Wildbolz 1958) and ovipositing moths may be attracted by the odor of apple fruit (Wearing et al. 1973). Neonate larvae also must locate host fruit when eggs are laid on foliage. Larvae may travel considerable distances (Steiner 1939) and contact fruit incidentally by random movement (Hall 1934). However, larvae may also be capable of locating host fruit by a combination of orientation behaviors, including chemotactic responses (McIndoo 1928, Sutherland 1972, Sutherland et al. 1974), thigmotaxis (McIndoo 1928) and by orientation to visual patterns (McIndoo 1929).

Sutherland (1972) demonstrated attraction of neonate codling moth larvae to odor of apple, using a closed arena-like test chamber (petri plate). Bradley & Suckling (1995) suggested that larval codling moth attraction to apples may be due to orthokinesis, klinotaxis or tropotaxis in response to α-farnesene. Following the terminology and explanations of Fraenkel & Gunn (1961), larvae may then encounter host fruit as a result of a change in the rate of locomotion (orthokinesis) in response to concentrations of this and other odorants from apple, or they may be capable of directed movement (taxis) towards the odor source. Taxis might be accomplished by larvae through the comparison of concentrations of a chemical with side to side head movements (klinotaxis) or by simultaneous comparison of concentrations at 2 or more receptor sites (tropotaxis).

Although experiments with arena (petri dish) bioassays clearly demonstrated

effects of apple odors and isomers of α-farnesene on codling moth larval behavior (i.e. Sutherland 1972, Bradley & Suckling 1995), it is not clear how *C. pomonella* larvae might use apple odor (α-farnesene) to find host fruit. It cannot be assumed that the behavior observed in these arenas is representative of what occurs in nature in moving air because the arena bioassays possessed no airflow and probably poorly defined concentration gradients. Chemoanemotactic responses (chemical modulation of responses to wind) are nearly always involved in insect attraction to chemicals (Kennedy 1977a). To understand how or if a larva may arrive at a host fruit in response to volatilized chemicals, we should verify that orientation occurs in response to apple odor or apple odorants in moving air.

The primary objective of this study was to determine if neonate codling moth larvae are attracted by apple odor in moving air. A secondary objective was to gain some understanding of the orientation mechanisms involved in any attraction response of larvae to apple odor. Using modified Y-tube and straight tube olfactometers, we demonstrated attraction of neonate codling moth larvae to odor from small immature apples in an airstream. We also showed greater larval motility in an olfactometer within which a wire was suspended, providing a substrate similar to a plant stem for larvae to traverse.

Both (E,E)- and (Z,E)-α-farnesene are found in organic solvent washes of apple fruit, with the (E,E)- isomer the dominant form present (Anet 1970; Bradley & Suckling 1995). (E,E)-α-farnesene from solvent washes of apple fruit (99.5% E,E- and 0.5% E,Z-) and both the (E,E)- and (Z,E)- isomers from synthetic sources were found to be attractive to neonate codling moth larvae in arena bioassays by Sutherland (1972), Sutherland & Hutchins (1973), and Bradley & Suckling (1995). Because of these previous findings, we also report here amounts of (E,E)-α-farnesene emitted from attractive thinning apples.

Materials and Methods

General Procedures.—Codling moth eggs were obtained on wax paper sheets from a laboratory colony maintained at the USDA, ARS, Yakima Agricultural Research Laboratory. Two to 3 hr before assays, egg sheets were shaken free of larvae and sheets were transferred to a clean plastic box. Larvae used in bioassays were taken from this box, ensuring that they were less than 3 hr old. Active larvae were transferred individually from egg sheets to the arena or olfactometer with a fine camel hair brush. Thinning apples (3 cm diam.) were obtained from a commercial Golden Delicious apple orchard in June, 1996. These were stored at 2° C until the day before assays (6 to 8 months) and were held in an open container in the laboratory at 22° C for 24 hours preceding use in tests.

Volatile chemicals emitted by apples were collected for bioassays and for quantitative analysis. Apples for volatile collections were handled as in bioassays. These were 3 cm diam thinning apples stored at 2° C for 8 months and placed in open containers at 22° C for 24 h preceding collections. Individual apples were placed in a wide mouth 460 ml glass jar, identical to the holding jar system used for olfactometer bioassays described below. The jar lid was made of 3 mm thick teflon sheeting, to which two (inlet and outlet) 6.4 mm stainless steel fittings were attached. Inlet air was passed through a hydrocarbon trap (#14633, Alltech Associates, Deerfield, IL) which was prewashed 3 times with 250 ml of dichloromethane and baked overnight in an oven at 180° C. Filtered air was directed into

the lower part of the jar with 6.4 mm OD teflon tubing. The jar outlet was attached to a 15 cm length of 6.4 mm OD teflon lined stainless steel tubing, which was bent 180° so that a collector trap could be attached vertically. Airflow was metered at 180 ml/min, with a collection time of 30 min per sample. Collector traps (Heath & Manukian 1992) used to trap organic volatiles were made from 4.0 cm long by 4.0 mm ID glass tubing and contained 20 mg of Super Q as the adsorbent. Collector traps were extracted with dicholoromethane into 250 µl glass vials, and brought up to 200 µl with dichloromethane. This procedure was carried out on 3 individual apples.

Gas chromatographic analyses were conducted using a Hewlett Packard Model 5890A Series II gas chromatograph, equipped with a split-splitless injection port and flame ionization detector. Helium was used as the carrier gas. Analyses were carried out in the splitless mode using a DB-1 capillary column (60 m × 0.25 mm) (J & W Scientific Inc.). The column was held at 80° C for 2 min and programmed to increase 20° C/min until reaching 200° C, and maintained isothermally thereafter. Confirmation of compound identity was obtained using mass spectroscopy. Mass spectra were obtained using a Hewlett Packard 5890 series II gas chromatograph with a model 5971 mass selective detector, with column and conditions as described above. A sample of E,E-α-farnesene synthesized by Heath et al. (1991) was used as a comparison standard for GC and GC-MS analyses.

Three assay designs were used to evaluate neonate larval codling moth responses to odor of codling apples. These were a closed petri dish (arena) assay modeled after that of Bradley & Suckling (1995), a Y-tube olfactometer, and a straight tube olfactometer. The arena assay consisted of 5.2 × 1.5 cm plastic disposable covered petri dishes, in which 5 larvae were placed (in the center) along with two 20 × 3 mm pieces of paper (20#, white, long grain, xerographic copy paper, Office Max Inc.) The papers were treated either with solvent or test samples in solvent. These pieces of paper were placed 3 cm apart to left and right of the petri dish center. For a period of 3 min numbers of larvae arriving at the papers were tallied and a count was made at the end of 3 min of how many larvae were on or in contact with the paper. The Y-tube olfactometer consisted of a 1.3 cm ID Y-shaped glass tube in which was suspended a 16 gauge stainless steel wire. Arms of the Y were 4 cm in length and the stem of the Y was 2 cm in length. Airflow was introduced into each arm of the Y and vented through the stem. Airflow through each arm was metered at 180 ml/min (9.5 cm/sec), purified through a hydrocarbon trap (Alltech Associates, Deerfield, IL) and was passed through a 460 ml glass holding jar before introduction into the arm. Test materials were placed in the holding jars. Larvae were placed one at a time on the wire suspended inside of the Y stem and were observed for 2 min. Larvae were scored for arriving 2 cm into one of the arms of the olfactometer within the 2 min time period. The straight tube olfactometer consisted of a pair of parallel glass tubes in which a wire was suspended and through which air was passed. Each tube was 1.5 cm ID by 15 cm long. Airflow into each tube was metered at 100 ml/min, purified through a hydrocarbon trap and was passed through a 460 ml glass jar before introduction into a tube. Larvae were placed on the wire at the downwind end of each tube and were observed for 2 min. Maximum distance upwind attained in 2 min was recorded for each larva.

Arena Bioassay.—Experiment 1. Using the bioassay methods of Bradley &

Suckling (1995), an experiment was conducted to test for larval orientation to a headspace sample from thinning apples. This experiment was conducted in a dark room, following the procedures of Bradley and Suckling (1995), with a fluorescent red lamp above for observations, at 23° C and 25 ± 5% RH. The apple headspace sample was tested, after quantitative gas chromatographic analysis, at a dose standardized at 100 nanograms of (E,E)-α-farnesene present. Each sample was assayed in 10 μl of methylene chloride. A 10 μl application of methylene chloride served as a control. For treatment and control applications, papers were held within a fume hood until solvent visibly disappeared (ca 10 sec), before beginning assays. The assay consisted of simultaneous presentation of a treated paper and a control paper in a petri dish with 5 larvae. This assay was replicated 10 times and treatment and control positions (left and right) were alternated between replicates. Numbers of larvae arriving on each paper and numbers on each paper at the end of 3 min were recorded per replicate.

Data were analyzed by a paired t-test to determine if differences in the numbers of larvae arriving at, or remaining at 3 min, on treated papers were significantly different than on control papers.

Y-tube Olfactometer Bioassays.—Experiment 2. Neonate codling moth larvae were tested for responses to odor of thinning apples in a Y-shaped olfactometer both with and without a wire suspended within the tubing. Three apples (3 cm diam) were placed in one glass jar of the olfactometer setup. The other glass jar remained empty. Using the Y-tube without the wire, five larvae were tested in sequence, the positions of the jars were switched (left to right), and five more larvae were tested in sequence. Following this, the procedure was repeated using a different Y-tube in which a wire was suspended throughout. This comparison was conducted on five days, providing 50 larvae tested per treatment. Between assay sets, glassware, tubing and wire downwind of the treatments were washed with acetone, baked in a convection oven for 30 min at 110° C, and aired for 20 + hr. Numbers of larvae responding to apple odor versus the system control were compared using a χ^2 test. Percent responses were analyzed by Wilcoxon's signed rank test to determine if larval responses differed with olfactometer design (with and without the wire).

Experiment 3. Neonate larvae were tested for orientation responses to greater humidity in the Y-tube olfactometer. Humidity was added to one side of the olfactometer by blowing air over a 10 ml glass vial containing 4 ml of HPLC grade water. This vial was placed inside the glass jar of one side of the olfactometer and inlet air was vented into the jar one cm from the water surface, through a 0.5 cm ID steel tubing. This method increased the system humidity from 20–25% to 70% RH, verified by direct measurement inside the tubing with a thermohygrometer (HI #8564, Hanna Instruments, Woonsocket, RI). The glass jar for the other olfactometer arm did not contain water. Five larvae were then tested in sequence for movement up either arm. The positions of the jars were then reversed and 5 more larvae were tested in sequence. This test was replicated 5 times, providing 50 larvae tested. Response data were analyzed by χ^2 test to determine if responses to humidified and non-humidified airflow in the olfactometer arms were significantly different.

Experiment 4. A comparison was made of 0, 1, 2 or 3 apples as an attractant source for neonate codling moth larvae in the Y-tube olfactometer. For each assay

set, 0, then 1, then 2, and then 3 apples were placed in the left jar while the right jar remained empty. For each treatment (no. of apples), 5 larvae were tested sequentially. Treatment and control positions were reversed and 5 larvae were again tested to airflow from over 0, 1, 2, and then 3 apples. This comparison was replicated 5 times, with one comparison conducted per day for 5 day. Response data for apple treatments (0, 1, 2, or 3 apples) were compared to data for the corresponding controls in the opposite olfactometer arm (0 apples) using a χ^2 test.

Straight tube olfactometer bioassay.—Experiment 5. Neonate larvae were tested in paired straight-tube olfactometers to determine if larvae move faster or farther upwind in response to apple odor compared to system airflow. This assay involved simultaneous testing of larvae in two tubes, with one tube carrying airflow from over 3 apples and the other tube carrying airflow passed through an empty jar (control). The experiment was begun with airflow from an empty jar entering the right tube and airflow from over 3 apples entering the left tube. Five larvae were tested in sequence in each tube. Each larva was observed for 2 min and the farthest distance attained upwind was recorded. The positions of the control and treatment jars were reversed and the series was conducted again. This experiment was conducted on 5 day, providing 50 larvae tested per treatment. Response data were compared by a paired t-test.

Results

The predominant peak in thinning apple headspace collections had a retention time of 11.5 min on the DB-1 capillary column. Its identity as (3E,6E)-3,7,11-trimethyl-1,3,6,10-dodecatetraene, or (E,E)-α-farnesene, was confirmed by comparison of retention times and the comparison of E.I. mass spectra with synthetic (E,E)-α-farnesene (Heath et al 1991). Electron impact mass spectra obtained on the natural and synthetic farnesene were comparable to reported spectra for α-farnesene contained in the National Institute of Standards and Technology Library (Gaithersburg, Maryland).

Emission rates of (E,E)-α-farnesene from single codling apples were 1.25 ± 0.23 micrograms per hour when apples were stored in an open container for 24 hours, following 6 to 8 months in cold storage.

Arena Assay.—Experiment 1. Neonate codling moth larvae arrived at filter papers treated with apple volatiles from a headspace sample significantly more often than at filter papers treated with solvent ($t = 2.61$, $P = 0.03$, df = 9) (Figure 1). After 3 min, mean numbers of larvae on filter papers treated with apple volatiles were significantly greater than numbers of larvae on filter paper treated with solvent ($t = 2.69$, $P = 0.02$, df = 9) (Fig. 1).

Y-tube olfactometer bioassays.—Experiment 2. Neonate codling moth larvae responded positively to the odor of apple, in both Y-tube olfactometer designs (Figure 2). Few larvae entered the olfactometer arm carrying only system airflow (no apple odor), while significantly greater numbers of larvae ($\chi = 8.5$, $P = 0.004$ without the wire, $\chi = 16.1$, $P = 6 \times 10^{-5}$ with the wire) moved into the arm carrying airflow from over 3 apples. Significantly greater numbers of larvae responded positively to apple odor in the olfactometer containing the suspended wire within the tubing, compared to apple odor in the olfactometer not containing wire ($z = 2.8$, $P = 0.005$). (Fig. 2).

Experiment 3. Neonate codling moth larvae did not exhibit a significant re-

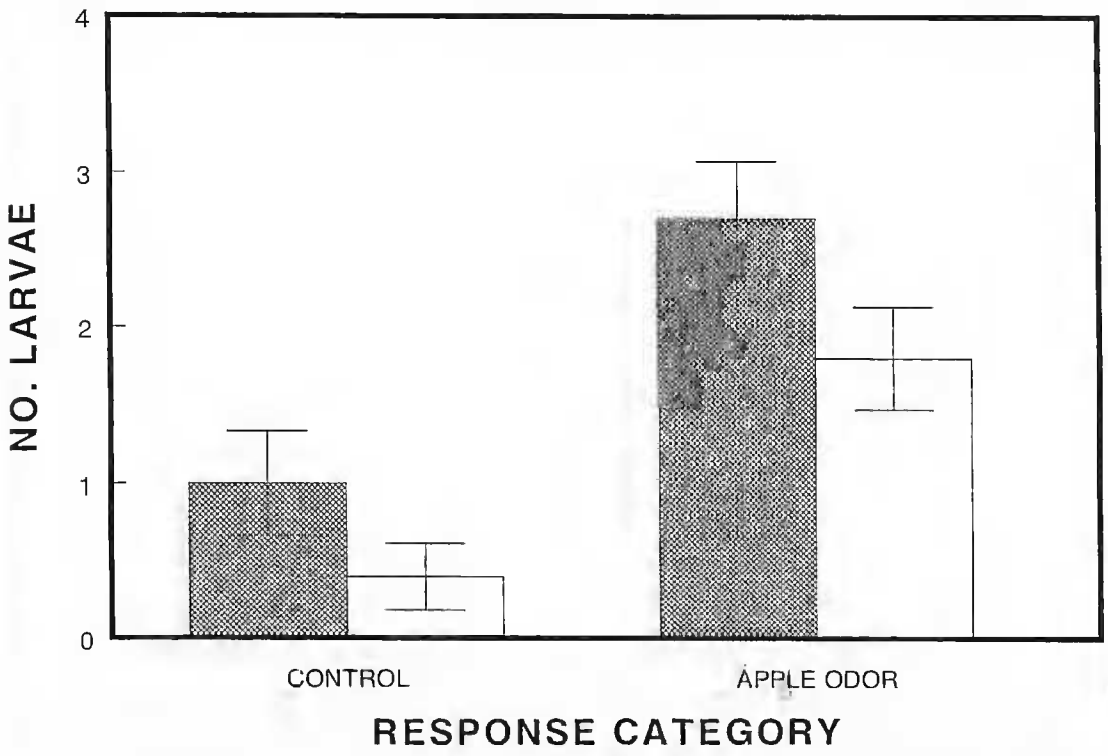

Figure 1. Mean (± SE) numbers of neonate codling moth larvae in a petri dish arriving at (cross hatched bars) 1.0 × 0.1 cm papers treated with solvent or apple headspace collection in solvent in 3 min, and mean numbers of larvae on those papers at the end of 3 min (open bars).

sponse to increased humidity in the Y-tube olfactometer. Numbers of larvae moving into olfactometer arms with humidified air and non-humidified air were not significantly different (44 vs 56% respectively) ($\chi^2 = 0.43$, $P = 0.51$).

Experiment 4. Significantly more larvae moved into the olfactometer arm carrying airflow from the jar of 3 apples compared to the control arm ($\chi^2 = 7.5$, $P = 0.007$, $n = 10$ for 3 apples) (Fig. 3). Numbers of larvae that moved into the olfactometer arm carrying airflow from jars with one or two apples were not

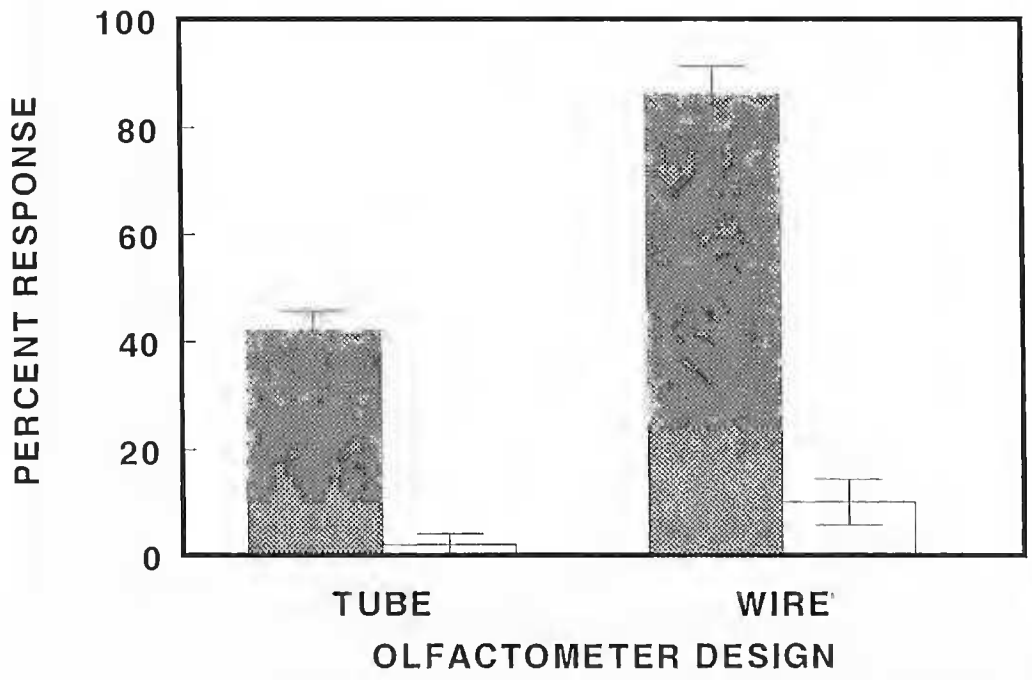

Figure 2. Mean (± SE) percentages of neonate codling moth larvae moving into the 2 arms of Y-tube olfactometers in response to airflow from an empty jar (open bars) or airflow from over 3 thinning apples in a jar (cross hatched bars). Olfactometers either were comprised of 2 cm glass tubing without a wire suspended inside, or consisted of 2 cm diameter tubing with a 16 gauge wire suspended in both arms as well as the stem of the Y.

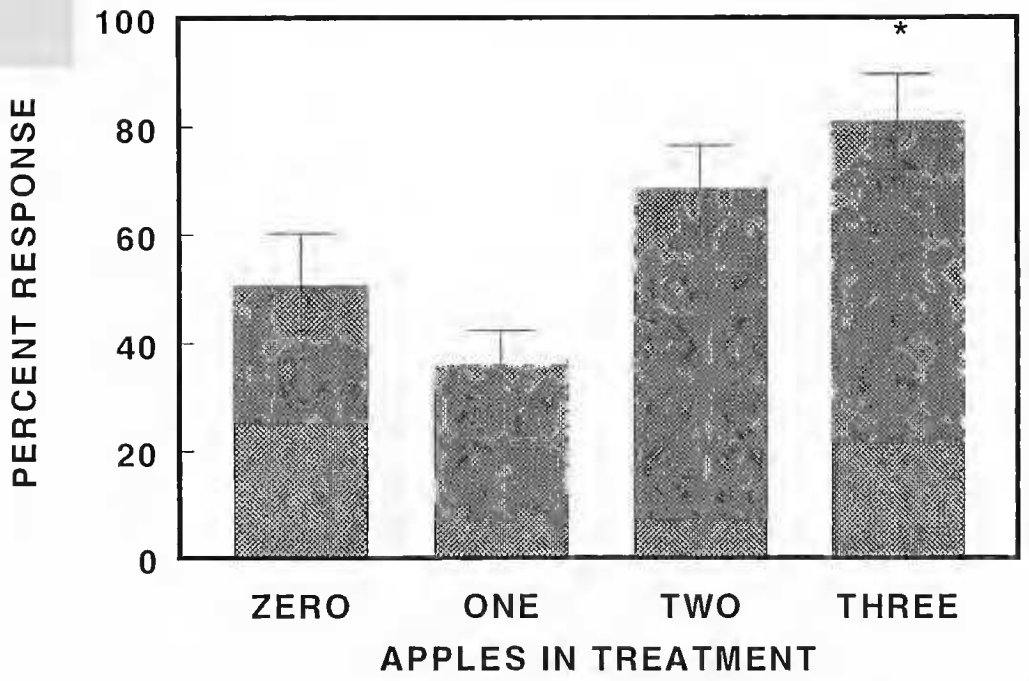

Figure 3. Mean (± SE) percentage of neonate codling moth larvae moving into a Y-tube olfactometer arm carrying airflow from zero, one, two or three codling apples. Bars with an asterisk are significantly greater than the control (zero apples) by a χ^2 test at $P < 0.05$.

significantly greater than numbers of larvae that moved into the corresponding control arm ($\chi^2 = 1.3$, $P = 0.25$, $\chi^2 = 2.7$, $P = 0.10$, respectively).

Straight tube olfactometer.—Experiment 5. The mean maximum distance upwind attained by neonate codling moth larvae in the olfactometer tube carrying airflow from over thinning apples was significantly greater than that attained by larvae in the tube carrying airflow passed through an empty jar ($t = 6.0$, $P < 10^6$). Larvae moved an average of 10.2 ± 0.4 cm in 2 min in tubes carrying apple odor, compared to 6.2 ± 0.5 cm in 2 min in tubes carrying system air without apple odor.

Discussion

Positive responses were obtained from neonate codling moth larvae to odor of apples in all three assay designs, shedding some light on behavioral mechanisms involving chemo-orientation that may be a part of larval codling moth host-finding. Significant numbers of larvae responded to paper strips treated with a sample of apple volatiles in the closed arena assay. This is in agreement with the findings of Sutherland (1972) that neonate codling moth larvae orient to apple odor, although our methods of presentation differed. Sutherland (1972) tested apple skin, apple flesh, and chloroform extract of apple, and we tested apple headspace volatiles. In our tests a response was evident both in cumulative numbers of larvae arriving at paper strips over the 3 min assay period, and in the number of larvae on paper strips at the end of the 3 min assay period. Bradley & Suckling (1995) suggested that larvae may orient to such treated strips by orthokinesis (changes in velocity with changes in chemical concentration) or by a taxis (a directed response resulting from comparison of stimulus intensities). The side to side head movements of larvae observed by Bradley & Suckling (1995) suggest klinotaxis rather than tropotaxis (Fraenkel & Gunn 1961).

Larvae responded positively to odor of thinning apples using the Y-tube olfactometer (experiments #2 and #4). Both ambulation upwind on the wire inside of

the olfactometer stem (carrying mixed airflow from both arms) and turning into the olfactometer arm carrying apple odor was necessary for a positive scoring in this assay. The responses of larvae to apple odor in the olfactometers likely involves either chemotactic or chemoklinokinetic responses as stated by Kennedy (1977b) at the junction of the two arms and stem of the olfactometer. A chemotactic response may be klinotaxis or tropotaxis, depending on the ability of the larva to compare odor intensities through side to side movements using a single receptor (indicating klinotaxis) or simultaneous comparisons using two or more receptors (indicating tropotaxis) (Fraenkel & Gunn 1961). The steep odor gradient expected at the junction of the olfactometer arms, where airflow carrying apple odor joined clean airflow, would permit comparisons by larvae of stimulus intensity over short distances. The experiments with Y-tube olfactometers were not designed to determine changes in larval speed or to determine if larvae move upwind in response to apple odor. However, there was a significant increase in upwind distance attained by larvae in the 2 min assay period when exposed to thinning apple odor in the straight tube olfactometer, indicating a greater forward speed. This response may be orthokinesis in response to apple odor. Codling moth larvae moved faster or farther upwind when detecting apple odor (orthokinesis) and turned into airflow containing apple odor (chemotaxis as klinotaxis or tropotaxis). Russ (1976) reported larval codling moth attraction to an extract commercially prepared from apple and pear fruit, using a Y-tube with airflow. Unfortunately observations of larvae were not made (larvae were checked after 24 h) and there did not appear to be experimental controls. Thus, it is difficult to interpret those findings in terms of larval behavior.

Positive responses to apple odor and upwind movement generally (treatment and control) occurred much more frequently in the Y-tube olfactometer when a wire was suspended within the tubing and larvae were placed on the wire rather than on the inside of the glass tubing. Neonate larvae on apple trees must traverse leaf, petiole, and stem surfaces in their search for host fruit. This modification to the olfactometer was thought to better approximate natural conditions for larvae, where moving over broad concave surfaces (such as the inside of glass tubing) rarely occurs. Although a 0.5 cm diam rod would better approximate an apple stem, the 16 gauge wire effectively increased the ambulation of larvae in these assays. This modification to the olfactometer may be useful for studying orientation responses of lepidopterous larvae generally.

The testing for response by larvae to increased humidity in the olfactometer was done to determine if positive responses to apple odor observed were due to increased humidity in the apple headspace. There was no indication of a response in the Y-tube olfactometer when 70% RH air was compared to ambient (20–25% RH) air, and it was concluded that responses to apple odor were not likely to be responses to increased water vapor in apple headspace.

The speed of larvae in the olfactometer assays was somewhat greater than that reported by Bradley & Suckling (1995). In the straight tube olfactometer, larvae generally moved 5–5.5 cm upwind during the 2 min assay, in response to apple odor. Larvae in the petri dish assays of Bradley & Suckling (1995) moved up to 1.5 cm per minute. This greater speed may be a result of directed movement (such as anemotaxis) by larvae in response to the odor gradients in olfactometers with airflow, versus nondirected movement (such as a kinesis) in the static air and poor

or nonexistent odor gradients in the petri dish (arena) assay. Greater larval movement in the olfactometer was also due in part to the addition of the wire to the olfactometer design possibly providing a superior substrate for larval locomotion.

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